

## IS *SIMULIUM TUBEROSUM* (DIPTERA: SIMULIIDAE) A PEST OF HUMANS? A PROBLEM OF INTERPRETATION AND SIBLING SPECIES<sup>1,2</sup>

J.F. Burger, L.A. Pistrang<sup>3</sup>

**ABSTRACT:** The *Simulium tuberosum* complex is known to consist of at least nine cytospecies throughout its Holarctic range, although some of these may prove to be only chromosomal segregates. The importance of members of this species complex as pests of humans is obscured by contradictory reports in the literature due to misidentification, geographically or seasonally variable biting habits, or the possibility that only certain cytospecies are attracted to humans. A study of the *tuberosum* complex in northern New York and New Hampshire, where high *tuberosum* populations occur, revealed that only 0.3 - 2.9% of adults collected while biting and annoying humans were *tuberosum*. This information, and a critical review of existing literature, demonstrate that adults of the *tuberosum* complex only occasionally bite or annoy humans, and are not major pests. Contradictory reports of annoyance in the southeastern United States cannot be confirmed without additional information.

*Simulium tuberosum* (Lundström) is a widely-distributed and often abundant Holarctic black fly. Studies of the polytene salivary chromosomes of *S. tuberosum* during the past 25 years by Landau (1962), Mason (1982, 1984), Adler (1986), and Adler and Kim (1986) demonstrated that this "species" is composed of at least nine chromosomally recognizable entities in the known geographic range, and that most of these entities are apparently reproductively isolated, i.e. biological species. Unless otherwise indicated, *S. tuberosum* is used in the broad sense, not in the strict sense. This information, and similar studies of other black fly species complexes, make a re-examination of published information on the biology, ecology and taxonomy of familiar, broadly-based morphospecies necessary. This is particularly important for those species considered to be pests of humans and livestock, since control efforts usually are directed at those species.

Contradictory published information about *Simulium tuberosum* as a pest of humans prompted a review of published information, and a study, reported here, conducted in New Hampshire and in northern New York, to determine if *S. tuberosum* was a major pest of humans. We also speculate on the possible causes for contradictory reports of *S. tuberosum* as a human pest species.

*Simulium tuberosum* occurs from Norway, Finland and Scotland to

<sup>1</sup>Received November 13, 1986. Accepted December 18, 1986

<sup>2</sup>Scientific Contribution Number 1460 from the New Hampshire Agricultural Experiment Station.

<sup>3</sup>Department of Entomology, Nesmith Hall, University of New Hampshire, Durham, New Hampshire 03824 U.S.A.

Greenland and Alaska south to California, Texas and Florida. The AB cytospecies is considered to be "true" *tuberosum* (Rothfels 1981) since it is the only one occurring in the type locality in northern Finland [Finnish Lapland]. It is also widely distributed in North America, from Alaska to Quebec, south to Alberta, Wisconsin and Virginia. The other sibling species described to date have a more limited distribution.

Reports on the habits of *S. tuberosum* vary from not attracted to or biting humans to being severe, persistent and important pests of humans. Contradictory information sometimes comes from the same geographic area, partly because some studies do not discriminate clearly between biting versus annoying [swarming, non-biting] flies, or do so in a manner difficult to interpret.

Some studies reported that *S. tuberosum* did not feed on humans (Smart, 1936 [Scotland]; Downe and Morrison, 1957 [Quebec]; Kuusela, 1971 [Finland]), or was not attracted to humans (Jenkins, 1948 [Alaska]; Zahar, 1951 [Scotland]). Raastad (personal communication) stated that *S. tuberosum* did not feed on humans in Norway.

Most authors stated that *S. tuberosum* was only occasionally attracted to or fed on humans, and was not a major pest species (Davies, 1952 [Ontario]; Hocking and Richards, 1952 [Labrador]; Wolfe & Peterson, 1960 [Quebec]; Anderson and DeFoliart, 1961 [Wisconsin]; Lewis & Bennett, 1973 [Newfoundland]; Lewis and Bennett, 1979 [Maritime Provinces of Canada]; Adler and Kim, 1986 [Pennsylvania]).

Several studies reported moderate biting or annoyance by *S. tuberosum* (Twinn, 1950 [as *S. perissum* Dyar & Shannon, northern Canada]; Davies *et al.*, 1962 [Scotland, 33% of *S. tuberosum* collected were positive for human blood]; Davies and Williams, 1962 [Scotland]; Davies, 1966 [Scotland]; Amrine, 1971 [Ohio]).

Some authors reported that *S. tuberosum* is a pest of humans only at certain times or in certain places (Stone and Jamnback, 1955 [New York, only until early July]; Peterson, 1956 [Utah]; Peterson, 1959 [Utah, above 7,000 ft (2,134 m)]; Abdelnur, 1968 [Alberta]).

Four studies listed *S. tuberosum* as a severe or major pest of humans (Edwards, 1915 [England]; DeFoliart, 1951 [New York, 1-15 bites per minute]; Stone and Snoddy, 1969 [Alabama]; Snoddy and Noblet, 1976 [southeastern U.S.A.]).

Several authors reported that *S. tuberosum* was annoying but did not bite (Jamnback, 1952 [New York]; Sailer, 1953 [Alaska]; Peterson, 1959 [Utah, below 2,500 ft. (762 m)]; Cupp & Gordon, 1983 [northeastern U.S.A.]). Others reported that *S. tuberosum* was attracted to but did not feed on humans (Sommerman *et al.*, 1955 [Alaska]; Jamnback and Collins,

1955 [New York, but mixed with *S. venustum* s. lat.]; Davies and Peterson, 1956 [Ontario]; Snow *et al.*, 1958 [Tennessee, Alabama, Mississippi, Georgia, North Carolina]; Magnarelli and Cupp, 1977 [New York]).

Two authors, Carlsson (1962) in Scandinavia and Fallis (1964) for Europe and North America indicated that *S. tuberosum* fed on mammals, with no specific mention of humans. Stone (1964) stated that the feeding habits of *S. tuberosum* could not be precisely determined in Connecticut since females could not be reliably separated from *S. venustum* Say and *S. verecundum* Stone & Jamnback.

## MATERIALS AND METHODS

To determine if *Simulium tuberosum* is a major pest of humans in northern New York, as reported in the literature, or in northern New Hampshire, where the immature stages are abundant in streams, we sampled 12 sites in New York on 14-16 June and 13-15 July 1982, and 10 sites in New Hampshire during spring and summer, 1982. In New York, we sampled 5 sites in Hamilton County (Blue Mountain to Long Lake, Newcomb, Minerva, and Tahawus), 6 sites in Essex County (Blue Ridge, New Russia, and Keene Valley), and 1 site in Clinton County (Ausable). We also examined 1,000 adult black flies selected from 44,800 adults collected during 1982 by Daniel Molloy and his colleagues at their Onchiota (Franklin County) study site. These samples were collected on 9-10 June, 5-6 July, 13 July, and 24-29 July, with no distinction made between flies attracted to collectors and those collected biting.

The principal sampling area in New Hampshire was Waterville Valley (Grafton County), where a concurrent study of the seasonal distribution and abundance of *S. tuberosum* sibling species in the Waterville Valley watershed was in progress, and where larval populations in streams were high. Additional collections were made from June through August at 9 sites in Coos County, New Hampshire.

Adult black flies were sampled by overhead net sweeps, 4 sets of 10 sweeps each, separated by 30 second intervals, during the morning and afternoon activity peaks. Biting flies were collected only after beginning to feed.

## RESULTS

In New Hampshire, 31 of 1,508 flies attracted to humans (Table 1) were *S. tuberosum* (2.3%), a percentage similar to that reported by Davies (1952) in Ontario, and Wolfe and Peterson (1960) in Quebec. Of 159 flies collected biting humans, 4 (2.5%) were *S. tuberosum*.

In New York, 5 of 1,433 flies swarming around humans in our collections (0.3%) were *S. tuberosum* (Table 2). Of 69 adults collected

biting humans, 2 (2.9%) were *S. tuberosum*. For the Onchiota study site (Table 3), 19 of 1,000 adults (1.9%) examined from all dates were *S. tuberosum*. At least 1 *S. tuberosum* adult was identified for each of the 4 dates examined, but more than half (11 of 19) were collected during the 5-6 July sampling period.

At no time did *S. tuberosum* exceed 2.9% of the flies attracted to or biting humans at any sampling station in New York and New Hampshire. We conclude, therefore, that *S. tuberosum* is not a major pest of humans in New York or New Hampshire, despite its abundance in small streams and larger rivers throughout the study areas, and need not be targeted for control in black fly abatement programs. The feeding habits of this reportedly anautogenous species group remain obscure in the northeastern United States.

Table 1. Adult black flies attracted to and biting humans in New Hampshire, May — September, 1982.

| Species                                                     | Biting | Swarming | Total |
|-------------------------------------------------------------|--------|----------|-------|
| <i>Prosimulium</i> spp. (3)                                 | 119    | 630      | 749   |
| <i>Simulium venustum</i> and<br><i>verecundum</i> complexes | 34     | 561      | 595   |
| <i>S. jenningsi</i> group                                   | 0      | 41       | 41    |
| <i>S. tuberosum</i> cpx.<br>(5 cytospecies)                 | 4      | 31       | 35    |
| <i>S. n. sp. nr. luggeri</i>                                | 0      | 33       | 33    |
| <i>S. parnassum</i> Malloch                                 | 1      | 23       | 24    |
| <i>Stegopterna mutata</i> (Malloch)                         | 0      | 15       | 15    |
| <i>S. decorum</i> Walker                                    | 0      | 8        | 8     |
| <i>S. corbis</i> Twinn                                      | 1      | 4        | 5     |
| <i>S. aureum</i> cpx.                                       | 0      | 2        | 2     |
| <i>S. vittatum</i> cpx.                                     | 0      | 1        | 1     |
| TOTAL:                                                      | 159    | 1,349    | 1,508 |

Table 2. Adult black flies attracted to and biting humans in the Adirondack Mountains, New York, June — July, 1982.

| Species                                 | Biting | Swarming | Total |
|-----------------------------------------|--------|----------|-------|
| <i>Simulium venustum</i> cpx.           | 34     | 782      | 816   |
| <i>S. verecundum</i> cpx.               | 29     | 520      | 549   |
| <i>S. jenningsi</i> group               | 0      | 141      | 141   |
| <i>S. tuberosum</i> cpx.                | 2      | 5        | 7     |
| <i>Prosimulium mixtum</i> Syme & Davies | 0      | 4        | 4     |
| <i>S. decorum</i> Walker                | 2      | 0        | 2     |
| <i>Stegopterna mutata</i> (Malloch)     | 0      | 1        | 1     |
| <i>S. longistylatum</i> Shewell         | 1      | 0        | 1     |
| <i>S. aureum</i> cpx.                   | 1      | 0        | 1     |
| TOTAL:                                  | 69     | 1,453    | 1,522 |

Table 3. Adult black flies attracted to a human host, Onchiota, Hamilton County, New York, 1982.

| Species                   | 9-10 Jun | 5-6 Jul | 13 Jul | 24-29 Jul | Total |
|---------------------------|----------|---------|--------|-----------|-------|
| <i>S. venustum</i> cpx.   |          |         |        |           |       |
| <i>S. verecundum</i> cpx. |          |         |        |           |       |
| <i>S. jenningsi</i> grp.  | 413      | 187     | 90     | 176       | 866   |
| <i>Prosimulium</i> spp.   | 49       | 0       | 1      | 1         | 51    |
| <i>S. vittatum</i> cpx.   | 20       | 3       | 3      | 2         | 28    |
| <i>S. parnassum</i> Mall. | 0        | 2       | 5      | 15        | 22    |
| <i>S. tuberosum</i> cpx.  | 5        | 11      | 1      | 2         | 19    |
| <i>S. pugetense</i> cpx.  | 8        | 0       | 0      | 0         | 8     |
| <i>S. corbis</i> Twinn    | 1        | 0       | 0      | 1         | 2     |
| <i>S. rugglesi</i>        | 0        | 1       | 0      | 0         | 1     |
| Nicholson & Mickel        |          |         |        |           |       |
| <i>S. decorum</i> Walker  | 0        | 0       | 0      | 1         | 1     |
| <i>S. aureum</i> cpx.     | 0        | 0       | 0      | 1         | 1     |
| <i>S. impar</i>           | 1        | 0       | 0      | 0         | 1     |
| Davies, Peterson & Wood   |          |         |        |           |       |
| TOTAL:                    | 497      | 204     | 100    | 199       | 1,000 |

## DISCUSSION

The results of our study agree with many other studies on the habits of adult black flies: that *S. tuberosum* only occasionally is attracted to or bites humans. How can we explain reports in the literature that *S. tuberosum* can be a serious pest of humans? This question is important because *S. tuberosum* larvae can be very abundant in streams and may be targeted for control efforts because they are purported to be pests of humans. If they are not major pests of humans, control may be unwarranted, at least until pest status can be established, with concomitant reduced control costs.

Reports on *S. tuberosum* as a human pest are contradictory not only throughout the range of this species complex, but also in the same geographic area. In Alaska, Jenkins (1948) reported that *S. tuberosum* was not attracted to humans. Sailer (1953), however, stated that it was annoying but did not bite humans, and Sommerman et al. (1955) stated that it was attracted to but did not feed on humans.

In the southeastern U.S.A., Stone and Snoddy (1969) and Snoddy and Noblet (1976) reported that *S. tuberosum* was a serious biting pest of humans, while Snow et al. (1958) stated that it was attracted to but did not bite humans.

In Scotland, Smart (1936) and Zahar (1951) reported that *S. tuberosum* was not attracted to humans, while Davies et al., (1962), Davies and



Williams (1962) and Davies (1966) stated that it caused moderate annoyance to humans. Edwards (1915) stated that it was a severe pest of humans in England.

Lewis Davies (personal communication) provided additional comments on the *S. tuberosum* group in the Skey Valley of the Central Scottish Highlands. Five black fly adults collected after feeding on a human in August, 1956, were *S. tuberosum*, but other records of human annoyance attributed to *tuberosum* may apply instead to *Simulium reptans* Meigen or perhaps to species in the *Simulium ornatum* group. *Simulium reptans* prefers to feed on cattle, rather than humans, while the reverse is true for *tuberosum*. *Simulium reptans* inhabits the lower reaches of streams where human habitation is more common, while *S. tuberosum* is found more commonly upstream where it is less likely to encounter humans. However, it seems clear that *S. tuberosum* in Scotland can be at least an occasional pest of humans.

Apart from imprecise definitions of *S. tuberosum* as a pest of humans, how can discrepancies in reports of this species group as a pest of humans be explained? Three explanations are possible.

First, other anthropophilic species (i.e. *S. venustum* and *S. verecundum* complexes) were misidentified as *S. tuberosum*. This could occur in several ways. Characters not suitable for reliable species distinction may be used, especially if they are variable. Use of inaccurate keys and figures may lead to misidentification. Reliable characters, such as features of the external genitalia, may be ignored because they are perceived as difficult to use. Misidentified reference specimens may be used to identify pest black flies. Reference in the literature to the difficulty of distinguishing *S. tuberosum* from other common pest species, such as *S. venustum* and *S. verecundum* (Stone, 1964), may discourage accurate identification of *S. tuberosum*, and encourage authors to "lump" it with other pest species. Reference in the recent literature to the "*venustum/verecundum*" complexes or the [*Prosimulium*] "*mixtum/fuscum*" complexes incorrectly implies that these complexes cannot be separated satisfactorily, and reflects the disinclination of certain workers to take the time necessary to examine genitalic and other characters.

*Simulium tuberosum* females are easily distinguished from *S. venustum* and *S. verecundum* females by the narrower fore tibiae bearing a pale streak on the anterior surface not extending across the entire width of the segment, and not forming a broad white patch, the narrow pale basal areas on the mid- and hind tibiae, and by the distinctive shape of the anal lobes.

Second, the biting habits of *S. tuberosum* may vary geographically, seasonally, or may be affected by local environmental conditions. It is well known that black fly biting intensity tends to increase as low pressure fronts

approach, prior to storms, but whether this occurs in all mammalophilic species is unknown. It is also possible that larval nutrition or environmental factors in streams may influence biting behavior of adult flies. It is difficult to assess the importance of geographic variation in biting/annoying habits of black flies without additional information.

Finally, some sibling species or chromosomal segregates in the *Simulium tuberosum* complex may be human pests, while others are not. Much of the information generated on the habits of *S. tuberosum* was published prior to definition of the sibling species (cytospecies) now known to comprise the *tuberosum* complex (Landau, 1962; Mason, 1982, 1984), or was not considered in discussion of *S. tuberosum* as a pest of humans.

Three cytospecies are known to occur in Europe: AB in Finland, and FGI and Y2 in Norway. Only in Scotland has *S. tuberosum* been recorded as a pest of humans, but since its cytogenetics has not been studied there, these biting records cannot be definitely associated with any of the known European cytospecies. Because the AB cytospecies is known to be widely distributed geographically and seasonally, it is possible that this cytospecies is associated with human annoyance in the Scottish Highlands. No records of human annoyance are published from the Scandinavian countries where FGI and Y2 occur.

In North America, human nuisance records are best known from Alaska, Alberta, Utah, eastern Canada, Wisconsin, New York, New Hampshire, Pennsylvania, and the southeastern United States. Three cytospecies are known to occur in Alaska: FGI, FG and AB. These also occur in Alberta, along with a fourth cytospecies, FGH. The cytogenetics of the *tuberosum* group has not been studied in Utah, but possibly the three widely distributed cytospecies occurring in Alaska occur there as well.

Seven cytospecies in the *S. tuberosum* complex are known from eastern North America (Table 4), although some of these may prove to be only

Table 4. Cytospecies of the *S. tuberosum* complex in Eastern North America.

| Ont. | Que. | Wis. | N.Y. | N.H. | Penn. | Va.  | S.C. |
|------|------|------|------|------|-------|------|------|
| AB   | AB   | AB   | AB   | AB   | AB    | AB   | —    |
| A    | —    | —    | A    | A    | A     | A    | A    |
| CDE  | —    | —    | CDE  | CDE  | CDE   | CDE  | —    |
| —    | CDEM | —    | CDEM | —    | CDEM  | CDEM | CDEM |
| —    | —    | —    | —    | —    | CKL   | CKL  | CKL  |
| FG   | FG   | —    | —    | FG   | FG    | —    | FG   |
| FGH  | —    | —    | FGH  | FGH  | FGH   | —    | FGH  |

chromosomal segregates within different populations and not biological species. Six of the seven cytospecies occur in the present New York-New Hampshire study area, and the seventh, CKL, is abundant in Pennsylvania, where Peter Adler's detailed studies on the ecology of black flies have greatly increased our knowledge of the *tuberosum* complex.

In New Hampshire, the FGH, FG and CDE cytospecies are abundant in montane streams, but since adults rarely were found biting or annoying humans during the past 10 years, these cytospecies cannot be considered important human pests. The A and AB cytospecies were collected less frequently, so their status as human pests is less certain.

In Pennsylvania, where all described eastern cytospecies occur, Adler and Kim (1986) stated that the complex was not a pest of humans, and that only a few instances of biting were recorded. This eliminates all the described eastern cytospecies as important human pests. How, then, can one explain the observation by Stone and Snoddy (1969) that *S. tuberosum* is the most persistent pest of humans and livestock in Alabama? Five cytospecies, A, CDEM, CKL, FG and FGH are known to occur as far south as South Carolina (Adler, personal communication) but none of these seems to be a human pest in northern localities. If their statement is correctly applied to *S. tuberosum*, the pest populations may be an undescribed cytospecies or based on misidentified material. Resolution of this problem must await analysis of the *tuberosum* complex in Alabama.

A final question is whether the occasional human nuisance or biting records cited throughout the geographical range of *S. tuberosum* s. lat. can be ascribed to one or two cytospecies, or whether several of them are involved. Only the AB cytospecies is common to areas where annoyance has been documented (except in the southeastern U.S.A.), and thus is likely to be at least an occasional human biter. Since it is not yet possible to positively identify adult female black flies by cytospecies, implication of *Simulium tuberosum* in human annoyance is not possible, except where only one cytospecies occurs.

In summary, *Simulium tuberosum* is not proven to be a major human pest species, and only rarely annoys or bites humans. In localities where biting records are carefully documented, none of the known *S. tuberosum* cytospecies can be considered a major human pest, in proportion to the large larval populations observed in streams. The pest status of the *S. tuberosum* complex in the southeastern United States, however, remains unresolved.

To clearly define the pest status of anthropophilic black flies, future studies should include careful identification of species and species complexes, clear reference to numbers of biting and swarming black flies, and a combination of cytotaxonomic and electrophoretic analysis of adults, when possible, to associate biting or annoying activity with a particular cytospecies.



## ACKNOWLEDGMENTS

We wish to thank R.W. Crosskey, Department of Entomology, British Museum (Natural History), L. Davies, Department of Zoology, University of Durham, J. Raastad, Zoological Museum, University of Oslo, and J.W. Amrine, Jr., Department of Entomology, West Virginia University for their generous contributions of information about the *Simulium tuberosum* group in England, Scotland and in Ohio, U.S.A., respectively. We also thank P.H. Adler, Department of Entomology, Clemson University for his valuable comments and for allowing us to use unpublished information about *tuberosum* in the southeastern United States, and P.C. Johnson and D.S. Chandler, Department of Entomology, University of New Hampshire for their reviews of this manuscript.

## REFERENCES CITED

- Abdelnur, O.M. 1968. The biology of some black flies (Diptera: Simuliidae) of Alberta. *Quaest. Ent.* 4: 113-174.
- Adler, P.H. 1986. Ecology and cytology of some Alberta blackflies (Diptera: Simuliidae). *Quaest. Ent.* 22: 1-18.
- Adler, P.H. and K.C. Kim. 1986. The black flies of Pennsylvania (Simuliidae, Diptera). Bionomics, taxonomy, and distribution. Pennsylvania State University Agr. Exp. Sta. Bull. 856.
- Amrine, J.W., Jr. 1971. The black flies (Diptera: Simuliidae) of Ohio. M. Sc. Thesis, Ohio State University, Columbus, Ohio.
- Anderson, J.R. and G.R. DeFoliart. 1961. Feeding behavior and host preferences of some black flies (Diptera: Simuliidae) in Wisconsin. *Ann. Entomol. Soc. Am.* 54: 716-729.
- Carlsson, G. 1962. Studies on Scandinavian black flies (Fam. Simuliidae Latr.). Opusc. Entomol. Suppl. XXI.
- Cupp, E.W. and A.E. Gordon, ed. 1983. Notes on the systematics, distribution and bionomics of black flies (Diptera: Simuliidae) in the northeastern United States. Search Agriculture No. 25.
- Davies, D.M. 1952. The population and activity of adult female black flies in the vicinity of a stream in Algonquin Park, Ontario. *Can. J. Zool.* 30: 287-321.
- Davies, D.M. and B.V. Peterson. 1956. Observations on the mating, feeding, ovarian development, and oviposition of adult black flies (Simuliidae, Diptera). *Can. J. Zool.* 34: 615-655.
- Davies, L. 1966. The taxonomy of British black-flies (Diptera: Simuliidae). *Trans. R. Entomol. Soc. London* 118: 413-511.
- Davies, L., A.E.R. Downe, B. Weitz and C.B. Williams. 1962. Studies on black flies (Diptera: Simuliidae) taken in a light trap in Scotland. II. Blood meal identification by precipitin tests. *Trans. R. Entomol. Soc. London* 114: 21-27.
- Davies, L. and C.B. Williams. 1962. Studies on black flies (Diptera, Simuliidae) taken in a light trap in Scotland. I. Seasonal distribution, sex ratio and internal condition of catches. *Trans. R. Entomol. Soc. London* 114: 1-20.
- DeFoliart, G.R. 1951. A comparison of several repellents against black flies. *J. Econ. Entomol.* 44: 265-266.
- Downe, A.E.R. and P.E. Morrison. 1957. Identification of blood meals of black flies (Diptera: Simuliidae) attacking farm animals. *Mosq. News* 17: 37-40.
- Edwards, F.W. 1915. On the British species of *Simulium* - I. The adults. *Bull. Entomol. Res.* 6: 23-42.
- Fallis, A.M. 1964. Feeding and related behavior of female Simuliidae (Diptera). *Exp. Parasitol.* 15: 439-470.
- Hocking, B. and W.R. Richards. 1952. Biology and control of Labrador black flies (Diptera: Simuliidae). *Bull. Entomol. Res.* 43: 237-257.

- Jamnback, H. 1952. The importance of correct timing of larval treatments to control specific blackflies (Simuliidae). Mosq. News 12: 77-78.
- Jamnback, H. and D.L. Collins. 1955. The control of blackflies (Diptera: Simuliidae) in New York. N.Y. State Mus. Bull. 350.
- Jenkins, D.W. 1948. Ecological observations on the blackflies and punkies of Central Alaska. Mosq. News 8: 148-155.
- Kuusela, K. 1971. Preliminary notes on the blackfly species (Dipt., Simuliidae) of Finland. Ann. Entomol. Fenn. 37: 190-194.
- Landau, R. 1962. Four forms of *Simulium tuberosum* (Lundstr.) in southern Ontario: a salivary gland chromosome study. Can. J. Zool. 40: 921-939.
- Lewis, D.J. and G.F. Bennett. 1973. The blackflies (Diptera: Simuliidae) of insular Newfoundland. I. Distribution and bionomics. Can. J. Zool. 51: 1181-1187.
- Lewis, D.J. and G.F. Bennett. 1979. An annotated list of the blackflies (Diptera: Simuliidae) of the Maritime Provinces of Canada. Can. Ent. 111: 1227-1230.
- Magnarelli, L.A. and E.W. Cupp. 1977. Physiological age of *Simulium tuberosum* and *Simulium venustum* (Diptera: Simuliidae) in New York State, U.S.A. J. Med. Entomol. 13: 621-624.
- Mason, G.F. 1982. Cytological studies of sibling species of *Simulium tuberosum* (Lundstrom) Diptera: Simuliidae. Can. J. Zool. 60: 292-303.
- Mason, G.F. 1984. Sex chromosome polymorphism in the *Simulium tuberosum* complex (Diptera: Simuliidae). Can. J. Zool. 62: 647-658.
- Peterson, B.V. 1956. Observations on the biology of Utah black flies (Diptera: Simuliidae). Can. Ent. 88: 496-507.
- Peterson, B.V. 1959. Observations on mating, feeding, and oviposition of some Utah species of black flies (Diptera: Simuliidae). Can. Ent. 91: 147-155.
- Rothfels, K.H. 1981. Cytotaxonomy: principles and their application to some northern species-complexes in *Simulium*, pp. 19-29 In Laird, M., ed. Blackflies: The Future for Biological Methods in Integrated Control. Academic Press Inc., New York.
- Sailer, R.I. 1953. The blackfly problem in Alaska. Mosq. News 13: 232-235.
- Smart, J. 1936. Notes on Simuliidae occurring at Fortingal, Perthshire. Scott. Nat. 217: 22-26.
- Snoddy, E.L. and R. Noblet. 1976. Identification of the immature black flies (Diptera: Simuliidae) of the southeastern U.S. with some aspects of the adult role in transmission of *Leucocytozoon smithi* to turkeys. South Carolina Agr. Exp. Sta. Tech. Bull. 1057.
- Snow, W.E., E. Pickard and J.B. Moore. 1958. Observations on blackflies (Simuliidae) in the Tennessee River Basin, J. Tennessee Acad. Sci. 33: 5-43.
- Sommerman, K.M., R.I. Sailer and C.O. Esselbaugh. 1955. Biology of Alaskan black flies (Diptera: Simuliidae) Ecol. Monogr. 25: 345-385.
- Stone, A. 1964. Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. Ninth Fascicle. Simuliidae and Thaumaleidae. Bull. Connecticut State Geol. Nat. Hist. Survey 97: 1-126.
- Stone, A. and H. Jamnback. 1955. The black flies of New York State (Diptera: Simuliidae). New York State Mus. Bull. 349.
- Stone, A. and E.L. Snoddy. 1969. The black flies of Alabama (Diptera: Simuliidae). Alabama Agr. Exp. Stn. Bull. (Auburn University) 390.
- Twinn, C.R. 1950. Studies of the biology and control of biting flies in northern Canada. Arctic 3: 14-26.
- Williams, C.B. 1962. Studies on black flies (Diptera: Simuliidae) taken in a light trap in Scotland. III. The relation of night activity and abundance to weather conditions. Trans. R. Entomol. Soc. London 114: 28-47.
- Wolfe, L.S. and D.G. Peterson. 1959. Black flies (Diptera: Simuliidae) of the forests of Quebec. Can. J. Zool. 37: 137-159.
- Zahar, A.R. 1951. The ecology and distribution of blackflies (Simuliidae) in south-east Scotland. J. Anim. Ecol. 20: 33-62.